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Diatom-based reconstruction of trophic status changes recorded in varved sediments of Lake Żabińskie (northeastern Poland), AD 1888-2010

by

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Abstract

We investigated diatom assemblages in surface sediments of 46 lakes in northern Poland and developed a diatom-based transfer function to infer epilimnetic total phosphorus (TP) concentrations. Multivariate ordination techniques (DCA, CCA) were used to identify major environmental gradients and to evaluate the effect of environmental parameters on the distribution of diatoms in the modern diatom dataset. The transfer function was developed using PLS, WA and WA-PLS models, and applied to a varved sediment core from Lake Żabińskie, AD 1888-2010. Annually-resolved quantitative reconstruction of TP concentrations shows that multidecadal changes in the TP level reflect the local settlement history, land-use changes and development of agriculture and tourism. The period of high trophic levels with maximum values of TP was documented until the late 1920s. In the 1930s-1970s period, TP generally decreased and eutraphentic flora was partly replaced by oligotraphentic and oligo-mesotraphentic diatom taxa. The reconstructed TP concentrations have started to increase from the 1970s. After the 1950s, strong short-term fluctuations of TP values were noted and explained by interactions between meteorological conditions, water column mixing and nutrient cycling in the lake.

Key words: diatoms, trophic changes, varves, Lake Żabińskie, Poland

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Introduction

Lakes are regarded as very sensitive aquatic ecosystems. One of the most pronounced processes that reflect the lake sensitivity to environmental changes is eutrophication, which can be harmful to both aquatic life and human health (Harper 1992). Urbanization, agriculture, soil erosion, domestic, animal livestock and industrial sewage disposal have become the main sources of anthropogenic nutrient inputs (Hall & Smol 2010). As a result, Holocene natural eutrophication has been overprinted by anthropogenic eutrophication leading to the degradation of water quality (Anderson 1993). By the mid-20th century, the eutrophication problem has become widely recognized as one of the most important problems in the degradation of natural environments. The excessive use of fertilizers causes nutrient enrichment, which leads to an increase in primary production and, in consequence, reduced light transparency, hypolimnetic oxygen depletion, changes in biochemical cycles and biological structures, including the loss of biodiversity (Carpenter et al. 1998). One of the biggest problems is the growing toxicity resulting from large blue-green algae blooms (Briand et al. 2003). These effects were observed in many lake ecosystems on a global scale and led to the intensification of research on the mechanisms, directions and magnitudes of the trophic status changes in lakes (Hall et al. 1999; Jordan et al. 2002; Battarbee et al. 2005; Smith et al. 2006; Dodds et al. 2009).

Lake eutrophication is one of the most urgent problems in water management and regional development in northeastern Poland. Dramatic changes in trophic status of many lakes during the second half of the 20th century caused ecological problems which have also affected the economic situation in the region (Marszelewski 2005). However, public concerns regarding the state of the environment led to a general decrease in the amount of nutrients discharged into the lakes during the last 25 years (Siuda et al. 2014). This initiated the ecological recovery in some of the lakes already in AD 1995 and thereafter, which was manifested in the decreased concentrations of total phosphorus (TP) in the lake water and higher water transparency (Kauppinen 2013). In this context, reconstruction of eutrophication processes for lakes in northeastern Poland is important to determine the reference conditions for their trophic statuses and to provide scientific advice for restoration programs applied to these ecosystems.

Being the major component of algal assemblages, diatoms are excellent bioindicators in the ecological assessment of lake ecosystems (Battarbee et al. 2001). They are usually abundant in lake sediments, diverse and sensitive to numerous environmental factors, including physical (e.g. light, temperature, water transparency) and chemical (e.g. pH, alkalinity, nutrient availability) ones. Changes in concentrations and ratios of nutrients (N:P, Si:P) may lead to substantial transformations in the structure of diatom assemblages (Tilman et al. 1982). Diatom studies using combined qualitative and quantitative approaches have been used to assess the eutrophication trends and to determine the baseline levels of nutrients in lakes since the 1990s (Hall & Smol 1992; Bradshaw & Anderson 2001; Marchetto et al. 2004). Diatom-inferred total phosphorus (TP) transfer functions were helpful in estimating the epilimnetic TP concentrations in order to reconstruct the former trophic statuses of lakes (Lotter 1998; Bennion et al. 2001; Kauppila et al. 2002; Finsinger et al. 2006). However, in some geographical areas with very heterogeneous lakes and uneven coverage of environmental gradients of interest, the performance of local models may be insufficient. The accuracy of optima and tolerance ranges of diatom species can be improved by merging local datasets with those from other regions, such as those from the EDDI (European Diatom Database) Combined TP dataset (http://craticula.ncl.ac.uk/Eddi) (Reed 1998; Mills & Ryves 2012), which has a broad species and geographical coverage and statistical strength.

Despite the excellent potential of diatoms, high-resolution reconstructions of lake trophic conditions are still missing for northern Poland. Therefore, in this study, we developed a training set of 50 lakes in northern Poland to calibrate biotic proxies against environmental and climatic variables. Sediment traps and thermistors were deployed in the lakes, and regular field surveys were carried out to analyze aquatic environmental variables. The same training set has been successfully used to establish transfer functions for assemblages of chrysophytes and chironomids, both of which have shown a strong relationship with water chemistry and climate (Hernández-Almeida et al. 2015a; Larocque-Tobler et al. 2015; 2016). Due to underrepresentation of high-TP lakes in this training set, we also merged the Polish dataset with some lakes from the EDDI Combined TP dataset in order to increase the accuracy of the estimated TP optima and tolerance ranges, and to improve the reconstruction at the high-TP end.

Varved (annually laminated) lake sediments are particularly valuable archives for high-resolution environmental reconstructions (Zolitschka et al. 2015). In the recent survey of lakes conducted in northeastern Poland, a number of lakes with annually laminated sediment were found (Tylmann et al. 2013). These lakes provide unique opportunities for quantitative reconstruction of the trophic status of lakes at near-annual temporal scales. For example, Lake Żabińskie, situated in the central part of the Masurian Lake District, represents a sediment record that has already shown its large potential for high-resolution paleoenvironmental studies (Amann et al. 2014; Bonk et al. 2015a; Hernández-Almeida et al. 2015b).

The objectives of the present study were to (1) develop a transfer function from the Polish Training Set to infer total phosphorus TP concentrations from diatom assemblages and (2) to reconstruct changes in epilimnetic TP from diatom assemblages in the varved sediments of Lake Żabińskie occurring since 1890. We interpreted the changes in terms of both man-made and climate-induced environmental changes.

Materials and methods

Training set sampling

Northern Poland is a glacially overprinted region with diverse topography, a wide variety of glacial landforms, and common glaciofluvial deposits. More than 7000 lakes are located in the region. They have different morphometric features, hydrological regimes, water chemistries and trophic states. A training set of 50 lakes across northern Poland was designed by statistical analysis of 2913 lakes, including outlier detection and stratified balanced sampling as described in detail by Hernández-Almeida et al. (2015a). The spatial extent of the study area is large (52°31′-54°19′N, 14°37′-22°53′E), covering about 600 km from the westernmost to the easternmost lake (Fig. 1). The selected lakes are located below 260 m a.s.l. They are deeper than 6 m, with moderate agricultural activity and/or forestry carried out in the catchments.

In October-December 2011, integrated sediment traps (PVC-liners with a length of 80 cm and a diameter of 9 cm, 2 tubes per trap) were deployed in the deepest parts of the 50 lakes, with the openings of the traps approximately 1.5 m above the lake bottom. After one year of sediment-trap exposure, 37 traps were found and recovered and 13 were lost. In order to maintain the original size of the training set, the surface sediment layers representing approximately 1-year deposition were sampled with a Uwitec corer in those 13 lakes. For the diatom dataset, 46 samples were finally used. Measurements of physical and chemical parameters in the water column (temperature, conductivity, oxygen, pH and turbidity) were performed at 1-m water depth intervals using a YSI 6820 meter (YSI, Yellow Spring, OH, USA). Surface and near-bottom water samples were collected using a Van Dorn water sampler at water depths of 1 m and 1 m above the lake bottom. Samples were placed in 1 l polyethylene bottles, transported to the laboratory and stored at 4°C prior to analysis. Concentrations of the main ions (Ca^{2+}, Mg^{2+}, N^{+}, K^{+}, sulfates, fluorides, chlorides) were determined by ion chromatography (ICS 1100, Dionex, USA). HCO_3^- was measured by standard titration methods. Total phosphorus (TP) and total nitrogen (TN) analyses were performed after mineralization of samples, using the colorimetric method and a Spectroquant NOVA 400 spectrophotometer (Merck).

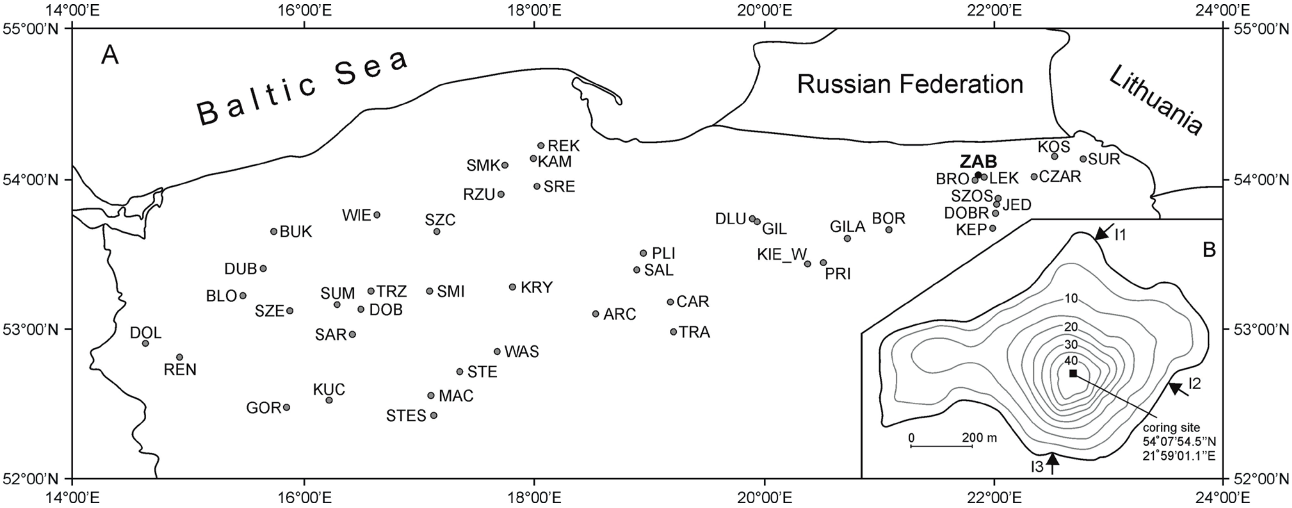

Figure 1

Location of lakes included in the Polish Training Set and Lake Żabińskie

In an attempt to have better coverage of the TP gradient, which at high TP (>2.2 $\log_{10}$ TP μg l^{-1}) is represented by only two lakes (Archidiakonka and Priamy), 25 additional lakes were integrated into the local dataset after taxonomic homogenization. Sites were selected to bridge the TP range from 2 to 2.7 $\log_{10}$ μg l^{-1}, and they correspond to lakes from the Central European, Danish, Northern Irish, United Kingdom meres, Southern England, Swiss and French datasets included in the continental EDDI Combined dataset. The use of these sites aimed to overcome the misrepresentation of high-TP diatom taxa in the fossil assemblages.

Lake Żabińskie sampling

Lake Żabińskie (54°07′54.5′′N; 21°59′01.1′′E; 120 m a.s.l.) is situated in the Masurian Lake District in northeastern Poland (Fig. 1). The lake has a surface area of 41.6 ha and the maximum water depth of 44.4 m. For diatom analysis, continuous subsamples were taken with annual resolution from a varved sediment core collected from the deepest part of the lake basin. Different methods for age estimation were applied, including varve counting, ^{210}Pb, ^{137}Cs, ^{14}C and tephra identification as presented in detail by Tylmann et al. (2016).

The preservation quality of the laminae was very good with clear sedimentary contacts between the laminae. In the lower part of the profile (69.5-48.2 cm), the thickness of varves ranged from 2.8 to 5.9 mm. The upper part (48.2-0 cm) consists of excellently preserved varves with a thickness ranging from 4 to 9.8 mm. Microscopic analysis of the varve microfacies and three independent counts enabled the estimation of a continuous chronology for the sediment profile from the year of core collection in AD 2011 until AD 1888 at 69.5 cm sediment depth.

Biogenic silica and diatom analyses

Biogenic silica (BSi) content was determined in homogenized and freeze-dried samples by the alkaline leaching method and ICP-OES measurements, corrected for lithogenic Si (Ohlendorf & Sturm 2008). Transformation of BSi concentration values into fluxes was made by multiplication of these values by the corresponding mass accumulation rate value. Samples for diatom analyses (ca. 0.1-0.2 g dry sediment) were prepared following the standard procedure for diatom observation under a light microscope (Battarbee 1986). The diatom samples were treated with 10% HCl to remove calcium carbonate. Next, the organic matter was digested using 30% H_2O_2, after which mineral matter was removed by decantation. To estimate the concentration of siliceous microfossils per unit weight of dry sediment (absolute abundance), a random settling technique was used (Bodén 1991). Permanent diatom preparations were mounted in Naphrax® (refractive index $n_D = 1.73$). The analysis was performed with a NIKON microscope under a 100× oil immersion objective. The counting method of Schrader and Gersonde (1978) was used, and 500 to 800 valves were counted in each sample to estimate the percentage abundance of particular taxa. The raw counts were transformed into relative abundance of the total frustules counted. The taxonomy and ecological information (habitat and trophic status) was primarily based on Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Denys (1991), Hofmann (1994), van Dam et al. (1994), Krammer (2000, 2002), Lange-Bertalot (2001) and Håkansson (2002).

Numerical methods

Multivariate statistical analyses were used to identify the main environmental gradients in the modern diatom dataset, and relationship between diatoms and their environmental variables. Prior to statistical treatments, diatom abundance was square-root transformed to stabilize their variance. Diatom species with a minimum relative abundance >2% and present in more than two samples were retained. Environmental variables were checked for skewed distribution, and all variables, except pH, were then $\log_{10}$ transformed. Detrended Correspondence Analysis (DCA) with detrending by segments and downweighting of rare species was performed on the species data to establish whether species distribution was unimodal or linear. A length of the DCA1 axis >2 Standard Deviation (SD) units indicates a non-linear unimodal response of organisms, while shorter gradients indicate a linear response (Hill & Gauch 1980; ter Braak 1995).

Canonical Correspondence Analysis (CCA) was performed to evaluate the effect of environmental parameters on the distribution of diatoms in the modern training set. The next step was to identify the environmental variable that explained most of the variance in the diatom dataset. Due to the fact that some environmental parameters are collinear, forward selection was used to assess the significance of each environmental parameter (individually) in explaining the maximum variation in the training set. Only significant variables at a 95% confidence level ($p<0.05$) were retained for subsequent analyses and considered in the second CCA. Individual CCA was also performed to estimate the individual importance of each parameter in explaining the variation in the training set. The ratio between the first constrained axis and the second unconstrained axis (λ_1/λ_2) was used to determine which environmental variable was most suitable for the transfer function development (Birks 1998). The diatom assemblage zones (DAZ) of the fossil dataset were identified using the constrained hierarchical clustering based on Euclidean distances to group only adjacent stratigraphic samples, which may correspond to major changes in the ecosystem (Legendre 1987). The ordination was performed using the R software (R Development Core Team 2009) with the add-on package VEGAN 2.3 (Oksanen et al. 2006).

The Transfer Function was developed using the following models: Partial Least Squares (PLS), Weighted Averaging (WA), using unweighted classical and inverse deshrinking and with/without tolerance downweighting, and Weighted Averaging – Partial Least Squares (WA-PLS). Performance was assessed by (leave-one-out) cross-validation (999 permutation cycles) (Birks 1995). The minimal adequate model was identified as having a combination of a high coefficient of determination (R^2) between observed and predicted values, a low mean and maximum bias, and a low root mean squared error of prediction (RMSEP). Concerning the PLS and WA-PLS model, only components leading to a reduction in RMSEP of 5% or more were retained (Birks 1995). The minimal adequate model was examined for potential outliers, based on visual inspection of the residual differences between predicted and observed values. Optima and tolerance of the species to the ecological variable of interest were determined using WA. Transfer functions were determined using the computer program C2 (Juggins 2003).

Results

Training Set – exploratory analyses, ordination and transfer function

Lakes in northern Poland were sampled along multiple environmental gradients (Table 1). Nutrient concentrations ranged from oligotrophic (TN) or mesotrophic (TP) to eutrophic. The first two PCA axes on the environmental data explained 55.2% of the total variation. The first axis (39.3%) was correlated with ionic composition (sulfates, Na, chlorides) and nutrients (TP and TN), while the second axis (15.9%) was correlated with pH, dissolved oxygen concentration and air temperature (Fig. 2). The Broken Stick model indicates that both the first and the second axis were significant ($p<0.05$).

Table 1

Basic statistics of morphometric features and water environment properties of lakes included in the Polish Training Set

		Min.	Max	Mean
Surface area	km^2	0.10	7.31	0.73
Max depth	m	6.00	43.6	16.0
Water temperature	°C	9.95	14.6	11.3
Specific conductivity	µS cm^{-1}	53.5	771	390
TDS[1]	g l^{-1}	0.03	0.50	0.25
Turbidity	NTU	2.18	23.0	5.42
pH		7.69	8.11	7.88
DO[2] concentration	mg l^{-1}	7.50	12.7	9.82
Na^+		1.65	23.9	7.46
K^+		0.46	16.2	3.93
Mg^{2+}		0.90	24.6	9.48
Ca^{2+}		6.01	127	60.4
HCO_3		0.30	5.32	2.77
SO_4^{2-}		4.72	136	29.8
F^-		0.07	18.9	0.55
Cl^-		2.45	74.2	15.4
N_{tot}		0.35	4.40	1.29
P_{tot}		0.02	0.33	0.08

[1]TDS – total dissolved solids, [2]DO – dissolved oxygen

A total of 169 diatom species, including varieties and forms, representing 45 genera were identified in the training set samples (Fig. 3). In all lakes, planktic diatoms prevailed, with frequencies ranging from 65 to 98%. In most cases, eutraphentic and eu-mesotraphentic taxa were abundant. *Stephanodiscus parvus* Stoermer & Håkansson dominates in 21 lakes (15-50%), *S. minutulus* (Kützing) Cleve & Möller in 16 (10-78%) and *Asterionella formosa* Hassal in 21 lakes (10-59%). *Aulacoseira ambigua* (Grunow) Simonsen dominates in six lakes (33-58%), whereas *Cyclostephanos dubius* (Fricke) Round in two lakes (23% and 29%). In six cases, the frequency of mesotraphentic and meso-oligotraphentic taxa with *Cyclotella ocellata* Pantocsek, *Fragilaria crotonensis* Kitton and *Puncticulata bodanica* (Eulenstein ex Grunow) Håkansson exceed in total 10%. Oligotraphentic species, i.e. *C. cyclopuncta* Håkansson & Carter, *C. polymorpha* B. Meyer & Håkansson and *Puncticulata praetermissa* (Lund) Håkansson, were common (7-33%) in five lakes. The benthic group represented by eutraphentic and eu-mesotraphentic species was noted permanently. In three lakes, *Fragilaria tenera* (W. Smith) Lange-Bertalot was the main component in the community (18-24%). In two lakes, *Cyclotella meneghiniana* Kützing and *Staurosira*

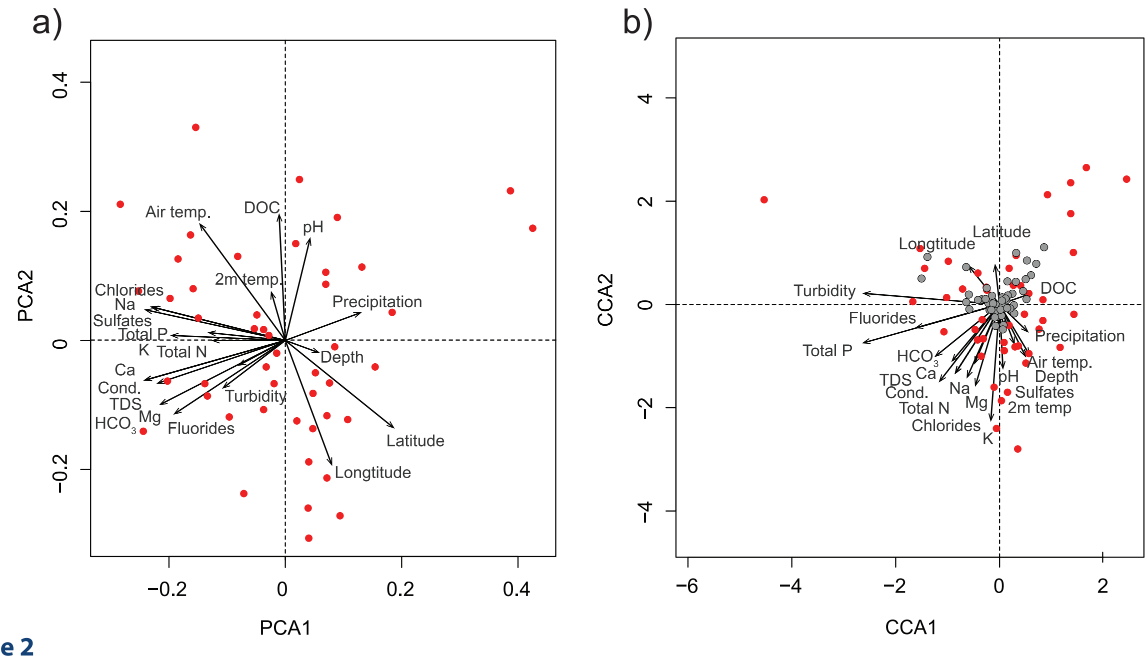

Figure 2

a) Principal component analysis (PCA) of all measured environmental variables in 46 lakes in Poland. b) Canonical correspondence analysis (CCA) based on 46 sites (red circles) and 57 species (grey circles)

construens (Ehrenberg) Williams & Round reached 22%. Moreover, *Amphora pediculus* (Kützing) Grunow, *Cocconeis placentula* Ehrenberg + varr., *Staurosira construens* and *Ulnaria ulna* (Nitzsch) Campère occurred in many lakes with low frequency.

DCA of the 46 Polish lakes in the diatom dataset revealed a gradient length of 2.6 SD, suggesting that unimodal methods were more appropriate for further analyses (Hill & Gauch 1980; ter Braak 1995). Results of the CCA analysis on the 46 lakes yielded CCA1 with

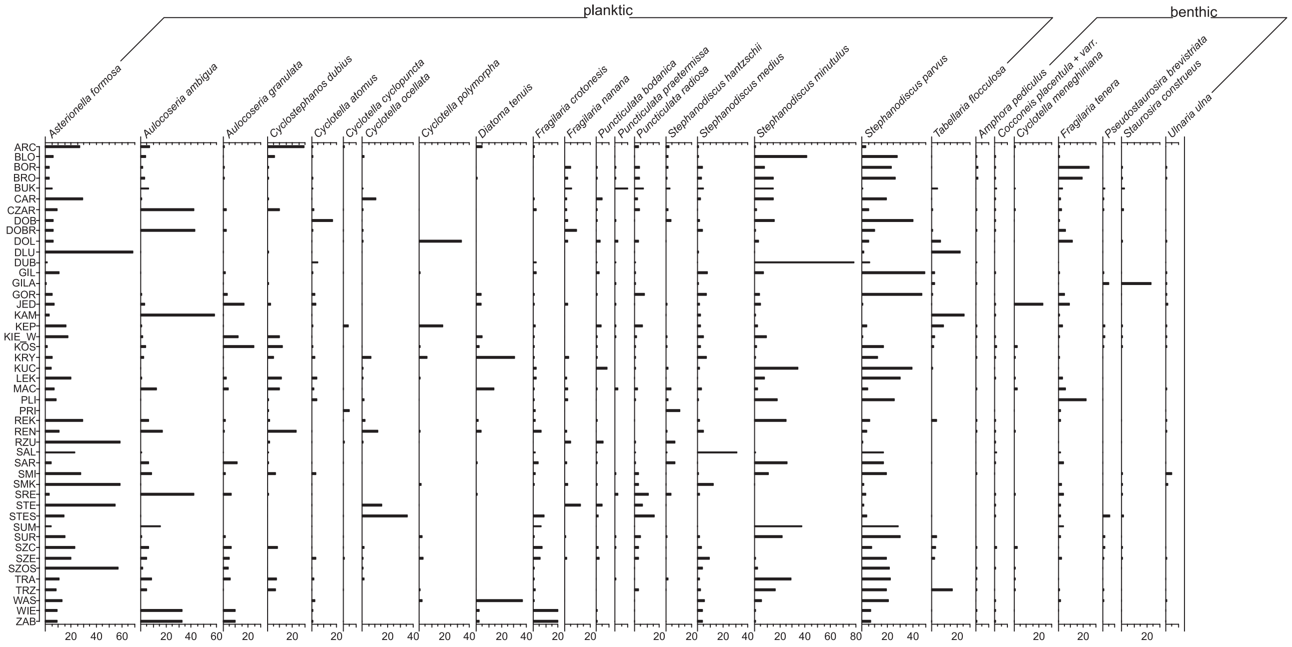

Figure 3

Diatom assemblages of surface training sets from 46 Polish lakes an eigenvalue of 0.146 (λ_1), accounting for 25.3% of the total variation in the diatom data, while CCA2 had an eigenvalue of 0.103 (λ_2), and accounted for 18.0% of the variation (Fig. 2). A subset of five significant environmental variables (conductivity, TP, K, HCO_3 and pH) was determined using forward selection. These variables account for 18.5% of the total variance in the diatom dataset, with TP explaining the largest portion of the total variance (5.2%), followed by conductivity and HCO_3 (both 4.8%), K (2.5%) and pH (1.2%). Individual CCA on these variables showed that TP had the highest ratio between the first constrained and the second unconstrained axis (λ_1/λ_2=0.6). Although λ_1/λ_2 larger than 1 is preferred to select a variable for a transfer function performance (Birks 1998), these results indicate that TP is the most important variable determining the diatom distribution in the Polish lakes.

Weighted Averaging (WA) with classical deshrinking and with tolerance down-weighting resulted in the best performing TP transfer function (Fig. 4a) for the Polish Training Set. The final model based on 46 sites had R^2_{cv} = 0.42, RMSEP = 0.22 $\log_{10}$TP and the Maximum

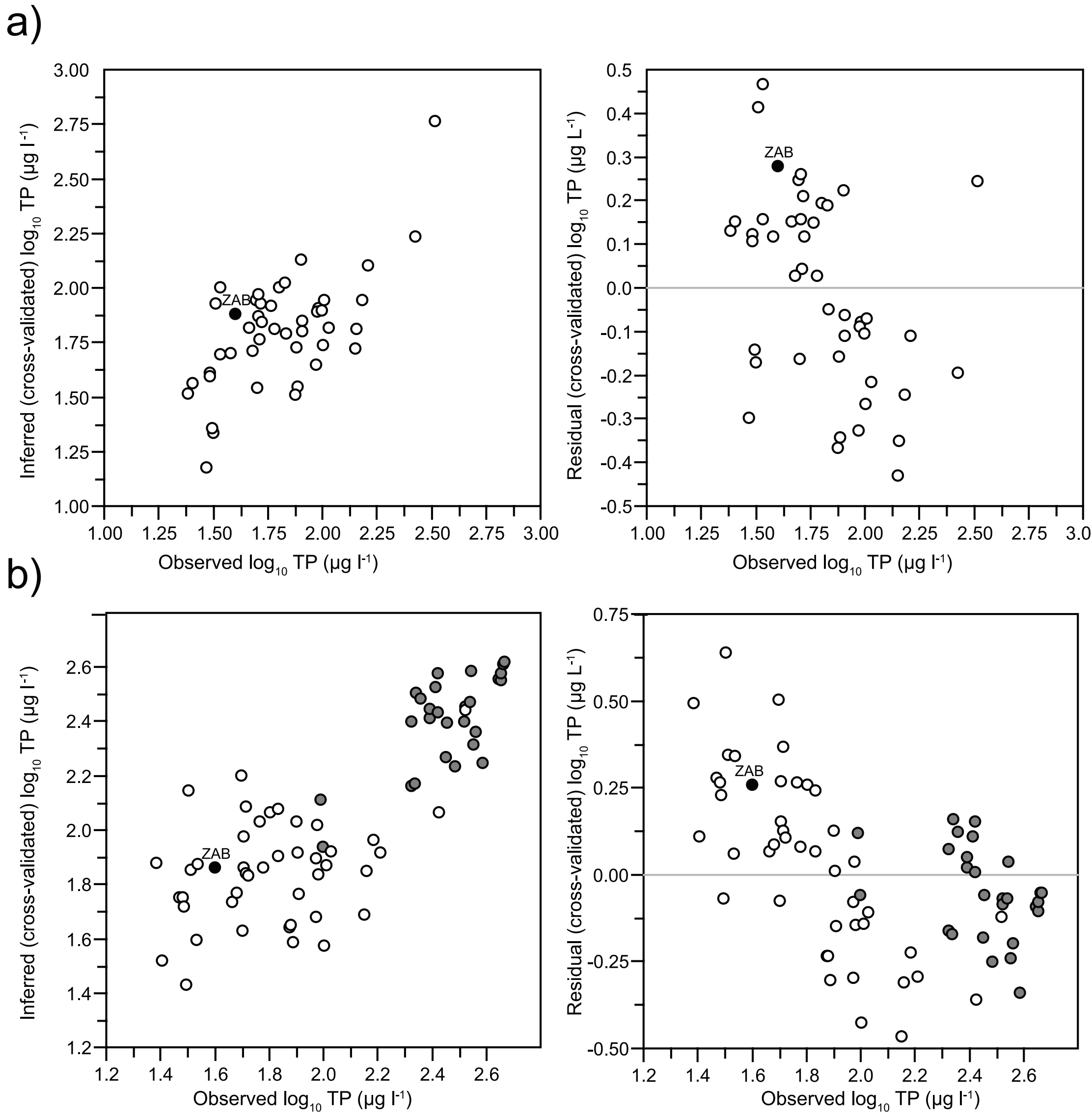

Figure 4

Plots of the observed versus predicted $\log_{10}$ TP and observed versus residual $\log_{10}$ TP based on: a) WA regression with classical deshrinking using 46 Polish lakes; and b) PLS-2 regression for 71 lakes (46 Polish + 25 EDDI). White dots represent lakes from the Polish Training Set, while grey dots are lakes from the EDDI training set. The black dot represents Lake Żabińskie, used in the reconstruction

Bias = 0.39. Simple WA was used to determine species optima and tolerance to TP. *Stephanodiscus tenuis* Hustedt was the most abundant species with the highest tolerance along the TP gradient, but with optima located at high-TP sites, while *Tabellaria quadriseptata* Knudson (agg.) was more common at low-TP sites. However, the best model for the merged Polish and EDDI dataset (71 lakes) was PLS with 2 components (Fig. 4b), yielding $R^2_{cv} = 0.66$, RMSEP = 0.22 $\log_{10}$TP and the Maximum Bias = 0.29. The fact that we obtained different models for different training sets is explained by the intermediate length of DCA1 (2.6 SD), in which both methods, linear and unimodal, perform well and can be used (Birks 1998).

Lake Żabińskie – biogenic silica

A biogenic silica flux shows a highly variable pattern along the profile (Fig. 5). In the lowermost part (AD 1888-1930), high values and variability of BSi fluxes are observed with a mean value and standard deviation of 0.033 and 0.016 g cm^{-2} yr^{-1}, respectively. The next section (AD 1931-1970) is characterized by lower fluxes of BSi (0.019±0.009 g cm^{-2} yr^{-1}). Subsequently, BSi increased in the next decade with the maximum of 0.059 g cm^{-2} yr^{-1} recorded in AD 1979. In the topmost part, BSi fluxes drop to minimum values within the entire profile.

Lake Żabińskie – diatom stratigraphy

Diatom fossils in the sediment sequence of Lake Żabińskie are abundant and well preserved. The absolute concentrations range between 1.2×10^6 and 165.5×10^6 valves cm^{-2} yr^{-1}. A total of 210 species, varieties, and forms belonging to 47 genera were recorded. The diatom assemblages were dominated by 49 planktic taxa. However, the benthic forms were more diverse (161 taxa). Constrained hierarchical clustering revealed the following five diatom assemblage zones (DAZ A-E) (Fig. 6, 7).

DAZ-A (AD 1888-1920). The diatom flora was dominated by planktic, alkalibiontic and eutraphentic taxa. In this group, *Stephanodiscus minutulus* reached the highest frequency (up to 62%). Less frequent were *Stephanodiscus neoastraea* Håkansson & Hickel and *S. parvus* (up to 22% and 25%, respectively). These species were accompanied by *Asterionella formosa, Aulacoseira ambigua, A. granulata* (Ehrenberg) Simonsen and *A. islandica* (O. Müller) Simonsen. The latter taxon achieved the highest abundance (up to 20%) at AD 1900. In the benthic group, species occurring in nutrient-rich waters (i.e. *Amphora copulata* (Kützing) Schoeneman & Archibald, *A. pediculus, Cocconeis placentula* with varieties, *Epithemia sorex* Kützing, *Fragilaria capucina* Desmazieres with varieties, *Rhoicosphaenia abbreviata* (Agardh) Lange-Bertalot, *Staurosira construens* and *Ulnaria ulna*) were also observed, but in very low percentages (ca. 1-2%). Diatom fluxes were high and variable (9.4-140.3 × 10^6 valves cm^{-2} yr^{-1}).

DAZ-B (AD 1921-1940). The main component of the diatom assemblage during this interval was still *Stephanodiscus minutulus*, ranging from 20% to 60%. *Asterionella formosa* and *Stephanodiscus parvus* were also observed, showing the highest abundance at AD 1933 (25%), and at AD 1939 (43%), respectively. Other species, *Stephanodiscus neoastraea* and *Aulacoseira islandica*, abundant in the previous interval, were replaced by *Diatoma tenuis* Agardh, *F. crotonensis*, *F. nanana* Lange-Bertalot and *Ulnaria acus* (Kützing) Aboal. The peak of *Stephanodiscus hantzschii* was recorded in the 1920s (17%). Eutraphentic and mesotraphentic benthos was represented mostly by *Achnanthidium minutissimum* (Kützing) Czarnecki, *Amphora pediculus*, *Cocconeis placentula* + varr., *Fragilaria capucina* + varr.,

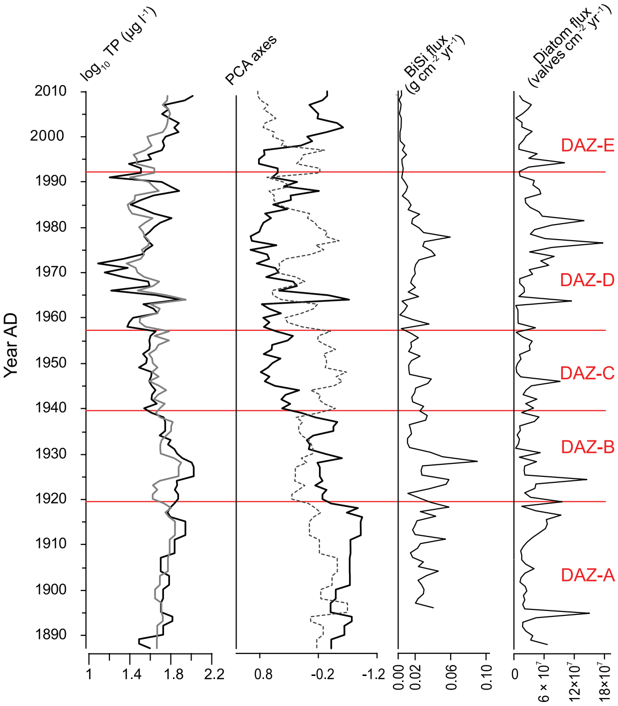

Figure 5

TP reconstructions (black solid line: Polish transfer function; grey solid line: Polish + EDDI transfer function) and PCA record (solid line: PCA1; dotted line: PCA2) versus BSi and diatom fluxes in Lake Żabińskie

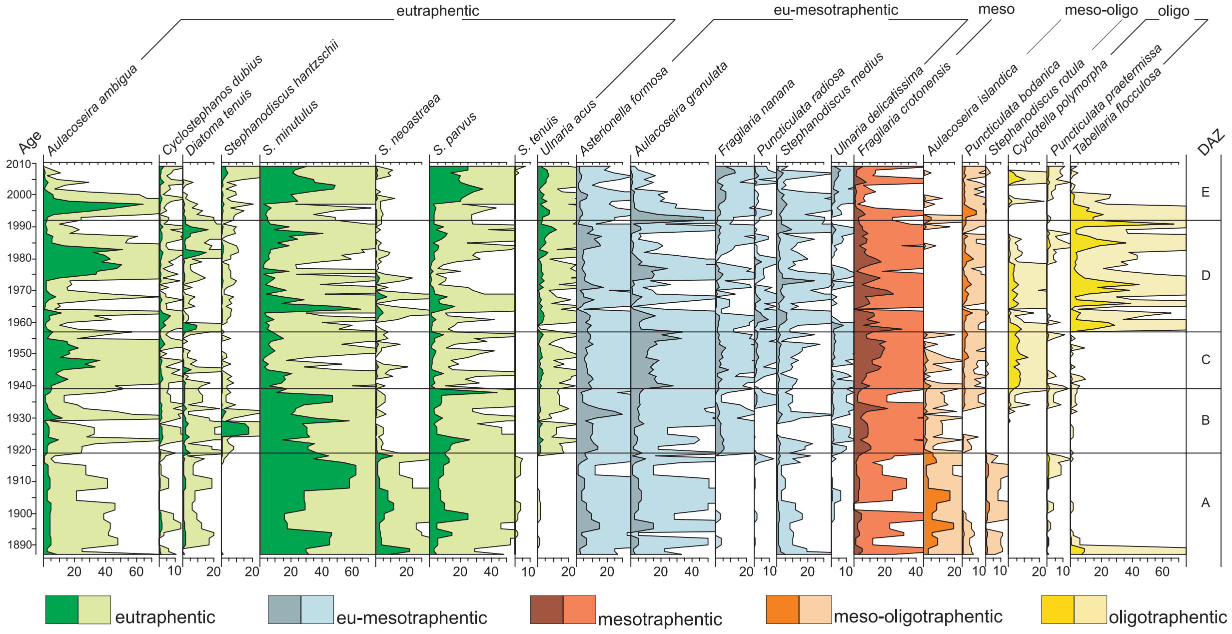

Figure 6

Diatom diagram with the main (more than 1%) planktic taxa in Lake Żabińskie. Trophic groups: eutraphentic (green), eu-mesotraphentic (blue), mesotraphentic (red), meso-oligotraphentic (orange), oligotraphentic (yellow); dark colors – frequency in percentage, light colors – frequency per mile

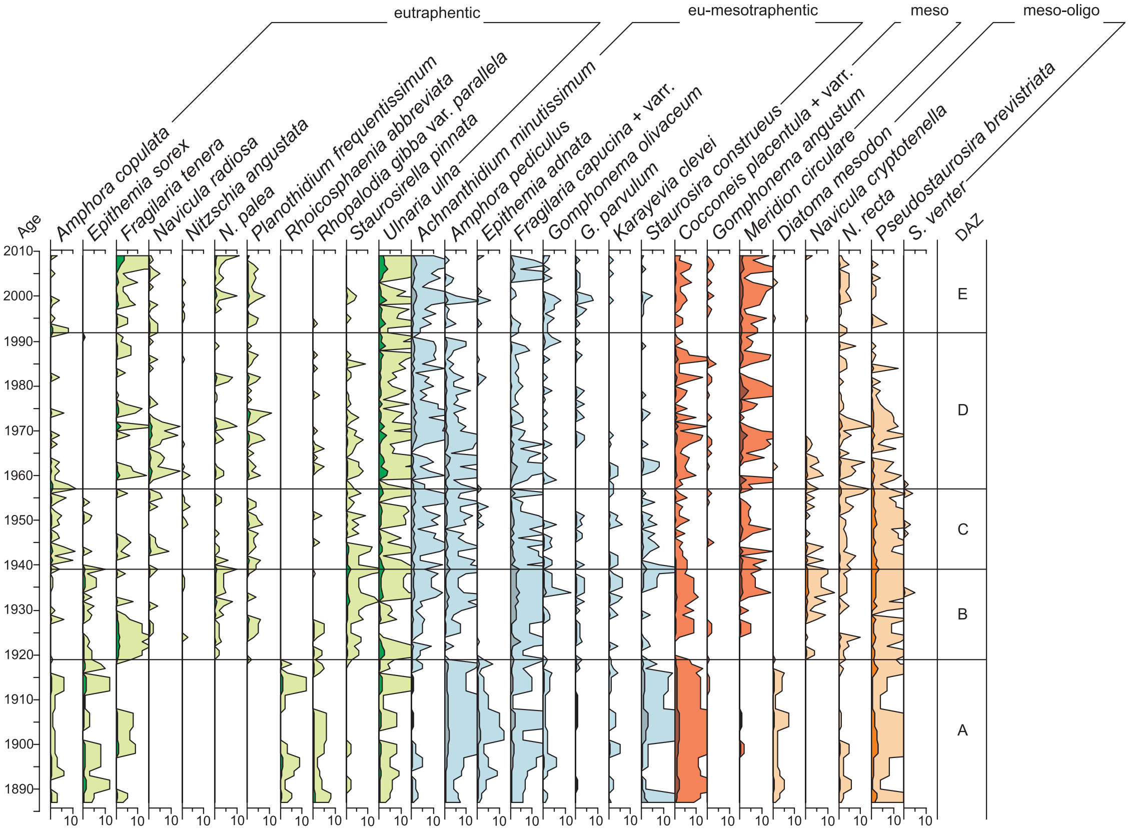

Figure 7

Diatom diagram with the main (more than 1%) benthic taxa in Lake Żabińskie, for explanations of colors see Fig. 6

Staurosirella pinnata (Ehrenberg) Williams & Round and *Ulnaria ulna*. Diatom fluxes were generally lower and in the range of 1.2-47.5 × 10^6 valves cm^{-2} yr^{-1} with one maximum of 135.3 × 10^6 valves cm^{-2} yr^{-1} in AD 1925.

DAZ-C (AD 1941-1958). In the 1940s and 1950s, the floristic composition shows clear changes. Representatives of the genus *Stephanodiscus* occurred rarely (up to 20%), whereas *Aulacoseira ambigua* and *A. granulata* were more frequent (up to 38% and 35%, respectively). At the same time, oligo- and mesotraphentic species, i.e. *Cyclotella polymorpha, Fragilaria crotonensis* and *Puncticulata bodanica* were observed more often. Moreover, some eutraphentic and mesotraphentic benthic taxa (i.e. *Cocconeis placentula* + varr. *Fragilaria capucina* + varr., *Staurosira pinnata*) were less frequent in this assemblage. Concurrently, the meso-oligotraphentic species *Nitzschia recta* Hantzsch and *Pseudostaurosira brevistriata* Williams & Round were noted. Diatom fluxes were similar to the previous interval and amounted to 2.0-85.0 × 10^6 valves cm^{-2} yr^{-1}.

DAZ-D (AD 1959-1992). The abundance of *Tabellaria flocculosa* (Roth) Kützing considerably increased during this interval and showed six peaks with abundance ranging within 30-70%. Three of the peaks correspond to the maxima of *Diatoma tenuis* (up to 10-16%). Small eutraphentic and eu-mesotraphentic diatoms, i.e. *Stephanodiscus medius, S. minutulus* and *S. parvus* occurred more frequently than before. The maximum frequency of *S. medius* at AD 1974 (24%) and two peaks of *S. minutulus* at AD 1965 and 1987 (65% and 24%, respectively) were recorded. *Aulacoseira granulata* occurred abundantly between the 1960s and 1970s, whereas *A. ambigua* showed the highest occurrence during the 1980s. At the same time, the abundance of diatoms typical for nutrient-poor waters, i.e. *Cyclotella polymorpha* and *Fragilaria crotonensis* gradually decreased. The frequency of other meso-oligotraphentic and oligotraphentic species (i.e. *Puncticulata bodanica, P. praetermissa*) was very low. Moreover, representatives of the genera *Amphora, Cocconeis, Fragilaria, Navicula, Planothidium, Staurosira* were rarely observed. Diatom fluxes were variable and significantly increased in the late 1970s (maximum of 165.5 × 10^6 valves cm^{-2} yr^{-1}).

DAZ-E (AD 1993-2010). At the beginning of this interval (AD 1993-1998), *Aulacoseira granulata* and *A. ambigua* had two peaks with abundance of 47% and 64%, respectively. Shortly afterward, these species were replaced by *Stephanodiscus minutulus* and *S. parvus*, which became the most abundant species until AD 2010, reaching up to 50% and 34%, respectively. They were accompanied by other eutraphentic and eu-mesotraphentic forms i.e. *F. nanana, Stephanodiscus hantzschii, S. medius, Ulnaria acus* and *U. delicatissima* (W. Smith) Aboal & Silva. Among the benthic flora, species indicative of nutrient-rich waters i.e. *Achnanthidium minutissimum, Fragilaria capucina* + varr., *F. tenera, Gomphonema olivaceum* (Hornemann) Brébisson, *G. parvulum* Kützing, *Nitzschia palea* (Kützing) Smith, *Planothidium frequentissimum* (Lange-Bertalot) Round & Bukhtiyarova and *Ulnaria ulna* occurred permanently. Diatom fluxes were lower than in the previous interval (1.6-93.3 × 10^6 valves cm^{-2} yr^{-1}).

Downcore TP reconstruction

The diatom-based TP WA and PLS-2 models using the Polish transfer function and the one merged with EDDI Combined TP, were applied to the fossil diatom assemblages from Lake Żabińskie (Fig. 5). Both reconstructions yielded very similar results and the correlation between them is very high ($r=0.75$; $p<0.05$). The reconstructions show a period of relatively high TP content with increasing trends until AD 1928-1929 followed by a period of gradual decrease in TP content until the lowest values recorded in AD 1973. Subsequently, the time interval AD 1974-2010 with a slightly increasing trend was observed again. Interestingly, despite the increasing trend in the recent period, both reconstructions show the highest TP values at the end of the 1920s. Apart from these multidecadal trends, significant differences in the interannual variability occurred. Relatively higher variability is observed until ≈AD 1939 compared to AD 1939-1953 with more stable TP concentrations. Much larger variability, with several considerable maxima (e.g. AD 1965, AD 1989 and AD 2010) and minima (e.g. AD 1967, AD 1973, AD 1986 and AD 1992), is observed from AD 1953 onwards.

DCA on the fossil diatom assemblage from Lake Żabińskie indicates that the ecological gradient length was 1.62 SD and, therefore, linear methods (PCA) can be used (Hill and Gauch 1980; ter Braak 1995). The comparison between the reconstructed TP and the scores of the first two PCA axes of the fossil data are shown in Fig. 5. The correlation between the TP reconstruction and PCA1 is $r = -0.67$ for the Polish Training Set, $r = -0.71$ for the merged one, at $p<0.05$, while it is not significant for PCA2. We also tested the relationships between the fossil diatom dataset and different climate variables, including annual and seasonal temperature, precipitation and wind. Among the few statistically significant relationships, the strongest correlation was found between PCA1 and warm-season (May-October) zonal wind speed (r=0.53; $p<0.05$; 3-yr filtered).

Discussion

Changes in the trophic status

Nutrients in lake waters can originate from external and internal sources. The external inputs of TP to Lake Żabińskie may come from the atmosphere through rainfall or dust deposition and from the catchment through inflowing creeks and surface overflow. Soil erosion in the catchment, agricultural practices (fertilizing) and wastewater from a recreation place seem to be the most important potential sources of TP. However, internal inputs i.e. recycling of nutrients within the water column and release of nutrients from sediments can also be an effective source of nutrients in the water body of deep lakes (Özkundakci et al. 2011). These processes might be efficient in the water column of Lake Żabińskie as the hypolimnion of this lake is mostly anoxic during the year with TP concentrations much higher in the hypolimnion than in the surface waters and the photic zone. Moreover, mixing patterns may change from year to year depending on the meteorological conditions (Bonk et al. 2015a). Therefore, we suggest that long-term (decadal and multidecadal) trends and variability in the reconstructed TP concentrations may be explained by long-term historical land-use changes (and related nutrient sources) in the catchment. On the other hand, short-term (interannual) fluctuations of the reconstructed TP values could rather reflect different intensities of TP cycling and lake mixing regimes, which may be largely controlled by meteorological conditions (wind and temperature).

Accordingly, the reconstruction shows considerable temporal variability in the diatom-inferred TP concentrations in Lake Żabińskie (Fig. 7). Interestingly, changes in the last 120 years do not display a significant long-term trend such as the expected increases in eutrophication during the second half of the 20th century, which could be related to general intensification of agriculture and human impact in this region (Kauppinen 2013). This is well reflected by a different variability in the regional consumption of phosphate fertilizers and the reconstructed TP values (Fig. 8). Thus, our TP reconstruction reflects mostly local changes, which is not surprising given the small size of the catchment and the specific hydrological conditions. Hydrochemical analyses presented by Bonk et al. (2015a) show that the major inflow into Lake Żabińskie (I1, Fig. 1), which comes from the northeast and drains most of the catchment, is not

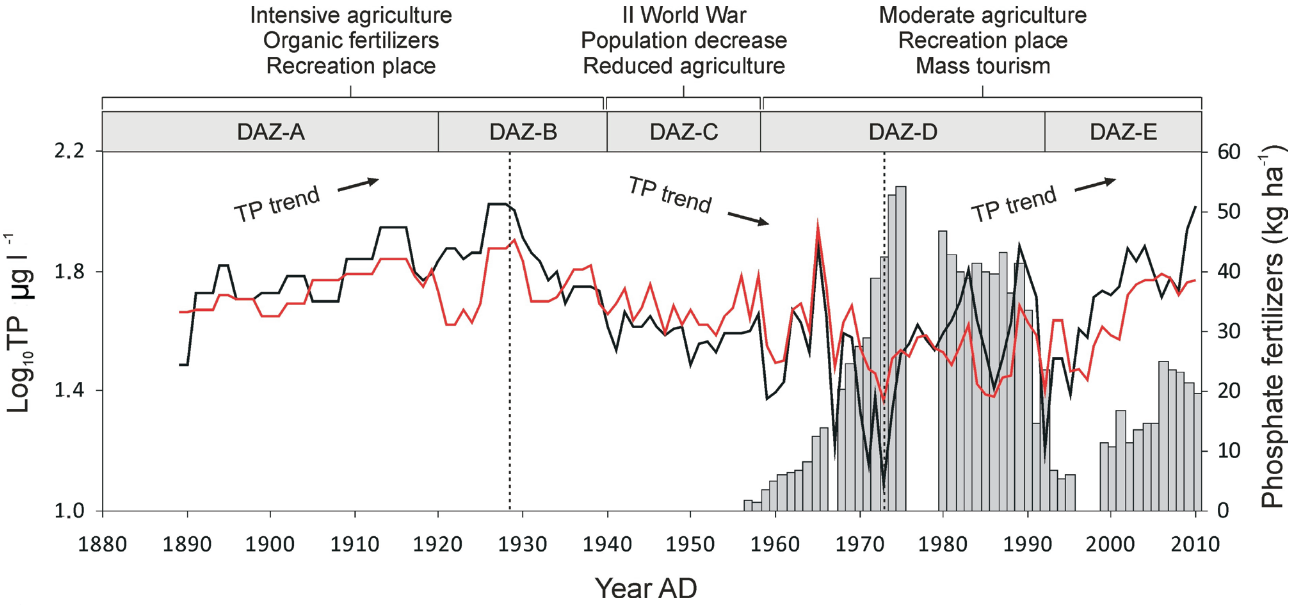

Figure 8

Comparison of TP reconstructions, regional consumption of phosphate fertilizers and major historical events in the catchment of Lake Żabińskie. Black and red lines represent TP reconstructions based on the Polish Training Set and merged Polish and EDDI datasets, respectively; grey bars represent fertilizers (data compiled from different statistical yearbooks, no data available for the period before 1957, and for the years 1967, 1976-1979, 1996-1998) a major source of nutrients transported to the lake. This is because Lake Purwin located upstream of Lake Żabińskie operates as an efficient sink for nutrients released from the catchment. According to the same authors, the highest concentrations of nutrients are found in the southern creek (I3, Fig. 1) which provides water from arable lands adjacent to the village of Żabinki located ca. 0.5 km south of the lake. Therefore, the local settlement history, land-use changes and development of agricultural practices in the area directly surrounding the lake may provide a reasonable interpretation of the TP reconstruction.

While there is no significant long-term trend for the entire period, opposite tendencies are visible for different time intervals. Already at the turn of the 19th and the 20th century, the concentrations of TP were relatively high and increasing until AD 1928-1929. In the diatom flora of DAZ-A, *Stephanodiscus minutulus* and *S. parvus* were the most important components. Additionally, species associated with nutrient-poor conditions (e.g. *Aulacoseira islandica;* Bennion et al. 1995) disappeared in DAZ-B, while a peak of eutraphentic species *S. hantzschii* was observed at the end of the 1920s. The high levels of TP in this period must have been related to intensive agriculture in the direct catchment of the lake. The village of Żabinki was founded in AD 1713. Stabilization of local settlements was associated with permanent deforestation of large areas and placement of fields and meadows in the lake catchment already in the 18th century (Wacnik et al. 2016). According to pollen analysis of the sediment record from Lake Żabińskie, most intensive agricultural activity in the direct vicinity of the lake started at the beginning of the 19th century and lasted until the late 1930s (Bonk et al. 2015b). At that time, agricultural practices involved extensive use of organic fertilizers (animal manures), which could have been an important source of phosphorus delivered to the lake. Additionally, a restaurant and a recreation place (campsite and beach) were established on the northern shore of Lake Żabińskie in the 1920s, which led to partial deforestation of the northern shore and provided additional inputs of nutrients into the lake. All of the above conditions support the reconstructed high level of TP during the early 20th century.

Starting from the 1930s, a decreasing trend in the reconstructed TP is visible until the early 1970s. This decrease results from lower percentages of the eutraphentic species *Stephanodiscus* spp., combined with the occurrence of oligotraphentic and meso-oligotraphentic diatom taxa e.g. *Cyclotella polymorpha* and *Puncticulata bodanica* in DAZ-C. The change to less eutrophic conditions may be explained by reduced agricultural practices and a lack of recreational activities during World War II. Evacuations, fights, and deportations of people from the Masurian region after AD 1944-1945 caused the depopulation of these areas which stopped agricultural practices. The recreation place was abandoned until the mid-1950s, when first recreational activities restarted. Despite the general decreasing trend in this period, the variability of TP content increases substantially from the late 1950s, which may indicate more intensive human impact after the time of stagnation. Massive occurrence of *Tabellaria flocculosa* in the early 1970s (up to 40%) influenced the TP reconstruction which shows the lowest TP concentrations for the entire analyzed period.

Since the 1970s, the small planktic group *Cyclotella* spp. was gradually replaced by *Stephanodiscus* spp. in DAZ-D. In the upper part of this zone, abundant occurrence of another eutraphentic species, i.e. *Aulacoseira ambigua*, accompanied by eu-mesotraphentic *A. granulata* was also observed. These changes are consistent with information about the development of the recreation center which was significantly enlarged in the early 1970s and in the mid-1980s when it became a popular holiday destination for large groups of tourists. During the most recent period (AD 1995-2010), *Aulacoseira* spp. and small *Stephanodiscus* taxa dominated, which indicate higher TP content: the modern values (AD 2006-2010) are the highest in the last 40 years.

Besides multidecadal changes, there are also substantial short-term (interannual) fluctuations of the reconstructed TP values. These fluctuations do not follow the intensity of agricultural development in the region or historical land-use changes in the catchment. Therefore, it is unlikely that they could be driven by changes in external inputs of phosphorus to the lake. Alternatively, different rates of internal TP loadings related to recycling of phosphorus within the water column might be responsible for this interannual variability. With this respect, the length and intensity of overturn periods as well as changes in the stratification stability during the warm season are especially important to the nutrient budget in lakes, because transport of nutrients from hypolimnetic waters to the surface largely controls the nutrient pool available in the epilimnion. Depending on the meteorological conditions, Lake Żabińskie may undergo four different scenarios of annual mixing patterns (Bonk et al. 2015a): (1) typical dimictic, (2) one complete mixing period in spring, (3) one complete mixing period in fall or (4) permanent stratification (meromixis). It was also demonstrated that green algae developed rapidly in spring, while in summer and fall they were gradually outcompeted and replaced by blue-green algae. During fall, however, another green algae bloom could appear depending on the intensity of the water column mixing. These complex relationships between meteorological conditions, water column stability and nutrient cycling must have influenced the diatom communities in Lake Żabińskie. The fact that PCA1 of the fossil diatoms is positively correlated ($r=0.54$, $p<0.001$) with May-October zonal winds at Lake Żabińskie may reflect the important role of water column stability in the development of diatom communities during the productive period (early spring/late fall). It is widely known that seasonal or interannual fluctuations of some diatom species can be explained by their responses to mixing patterns of the water column (Köster & Pienitz 2006). High turbulence induced by a strong wind can impact the development of elongated planktic species such as *Asterionella formosa, Diatoma tenuis, Fragilaria crotonensis* and *Tabellaria flocculosa* (Morabito et al. 2012). In addition, the settling velocity of these species is significantly reduced by their ability to form different types of colonies. Star-shaped colonies of *A. formosa*, zig-zag colonies of *D. tenuis* and *T. flocculosa* and ribbon-like colonies of *F. crotonensis* effectively prolong the growing period, which increases their relative proportions in the diatom community (Rühland et al. 2015). This might be especially important to our TP reconstruction since it looks very much affected by *Tabellaria flocculosa* in the topmost part of the sediments, which shows almost an inverse relationship with the TP reconstruction in DAZ-D (Fig. 7). Although this species is regarded as an indicator of early eutrophication, its long-term dynamics might not be strongly related to the changing trophic conditions as a result of land-use changes because it might be controlled by physical factors related to meteorological conditions, i.e. wind, air and water temperature (Morabito et al. 2012).

Especially for lakes with variable mixing patterns it is difficult to establish to what extent TP reconstructions present changes in external phosphorus inputs related to land-use change and how much they are affected by internal nutrient loadings related to lake mixing and, ultimately, to climate. In deep lakes, there are strong links between climate and nutrients, because temperature and wind are the main drivers of lake mixing. However, mechanisms governing these relationships and processes might be very complex and not stable in time (Kirilova et al. 2011).

Diatom-based TP transfer function

Over the recent years, the growing debate on the robustness of transfer functions indicated some of their fundamental weaknesses (Juggins 2013). This includes also reconstructions of epilimnetic TP using diatoms (Juggins et al. 2013). The criticism emerged from the fact that the basic assumptions of the approach are often violated which might lead to misleading reconstructions. One major problem in the case of diatom-inferred TP is that the relationship between epilimnetic TP and diatom relative abundance might be associated with secondary variables (e.g. water chemistry, light availability, short-term climate variability, competition between algal groups etc.).

Water chemistry changes in the Polish Training Set lakes are primarily related to dissolved ions, dissolved oxygen concentration and nutrients (Fig. 2). These differences are likely related to different land uses, catchment geology, sources and chemistry of inflowing waters. Unfortunately, changes in the land use often affect both nutrient content and ionic compositions. Consequently, covariance of these two environmental factors is expected, and it may be difficult to determine which of the two factors diatoms respond to (Ryves et al. 2004). Changes in K, sulfates and other ions affect nutrient uptake by diatoms, altering the nutrient transport across the cell membrane (Bhattacharyya & Volcani 1980; Saros & Fritz 2000). CCA shows that both TP and some variables related to ion content in the Polish Training Set lakes are partially correlated. Therefore, ionic composition of waters is linked to nutrient distribution in the lakes, and hence it might affect diatom assemblages.

The disadvantage of the current Polish Training Set is a shortage of lakes with high TP concentrations (i.e. $>2.2 \log_{10}$ TP µg l^{-1}). As a result, two lakes with the highest TP content (Archidiakonka and Priamy) may drive the model. The inclusion of sites with high TP concentrations in the Polish Training Set could improve the model performance (R^2) and would add valuable information regarding high TP levels that could have existed in the past. This could be done by merging of different datasets to fill gaps in the environmental gradient which is a common procedure when developing diatom-based inference models (Reed 1998; Mills & Ryves 2012). However, there are potential problems related to the merging, such as taxonomical and methodological inconsistencies between the datasets (Birks 1995). To avoid this problem, the diatom taxonomy of selected lakes from the EDDI database was updated to match the one of the Polish lakes, with the help of images and morphological description available at the original EDDI site. The high similarity between both reconstructions is likely due to the good taxonomic consistency, as well as similar optima and tolerance between the diatoms from the Polish lakes and those included from the EDDI training set. In addition, the high similarity resemblance between PCA1 and both TP reconstruction scores indicate that shifts in the fossil dataset correspond with changes in the reconstructed TP, and hence this variable was important to the fossil diatoms from Lake Żabińskie in the past (Fig. 5).

Conclusions

A training set of 46 lakes in northern Poland was developed and used for a diatom-based transfer function for TP concentration. The model was applied downcore (1888 – 2010) in currently eutrophic Lake Żabińskie. Varved sediments allowed for the first annually-resolved and quantitative reconstruction of trophic changes inferred from lake sediments in northern Poland.

Distinct changes in diatom assemblages, diatom-inferred TP concentrations and BSi flux indicate substantial variability in the trophic status of Lake Żabińskie in the last 120 years. However, our TP reconstruction does not reflect long-term progressive eutrophication caused by human impact as noted in many European lakes in the second half of the 20th century. The lack of a clearly increasing trend can be an effect of eutrophic status of the lake already in the 19th century. Multidecadal changes in TP levels recorded in sediments of Lake Żabińskie are consistent with the local settlement history and related land-use change. During the first period (until the late 1920s), a slightly increasing TP trend was recorded with maximum values for the last 120 years. This increase was driven mostly by agricultural activities and development of tourism. In the 1930s-1970s period, the general trend of decreasing TP was noted and caused most probably by depopulation of the Masurian region during and after World War II and, in consequence, a collapse of agriculture and tourism. From the 1970s, reconstructed TP values show an increasing trend again. Short-term (interannual) fluctuations of TP values are difficult to interpret and can be related to interactions between meteorological conditions, water column mixing and nutrient cycling in the lake.

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